

THE LIFE HISTORY OF
HYPSOCHILA WAGENKNECHTI WAGENKNECHTI,
A SCARCE BUTTERFLY FROM THE ANDES OF
TEMPERATE CHILE (LEPIDOPTERA: PIERIDAE)

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Abstract.—*Hypsochila wagenknechti wagenknechti* from Chile is pivotal in the phylogenetic interpretation of the Andean Pierini because the adult appears to present a mixture of *Tatochila*- and *Phulia*-like characters. Its egg, larva, pupa, and aspects of its behavior and ecology are here described. Morphologically, the early stages are more like *Tatochila* than *Phulia*, but show some approach to the aberrant features of *Phulia* and *Pierphulia* in that the larva fails to eat its eggshell, is sluggish and rests on a silken mat, and the pupa is more rounded than any *Tatochila* yet described. The species is a Crucifer feeder, like *Phulia* and three of the five species-groups of *Tatochila*, but is unique among known Pierini of the region in laying small clutches of eggs.

This is the sixth in a series of papers describing the life histories of the Pierini of the Andean region. Of the nine endemic genera, previous treatments have covered *Reliquia* Ackery (Shapiro, 1978a), three species-groups of *Tatochila* Butler (Shapiro, 1978b, 1979, 1986a) and *Pierphulia* Field (Shapiro and Courtney, 1986), and papers are in preparation covering *Phulia* Herrich-Schaeffer, *Infraphulia* Field, and *Theochila* Field.

The genus *Hypsochila* Ureta is critical to the phylogenetic interpretation of the Andean Pierini, which have been taken as a monophyletic group by all previous workers (Field, 1958; Herrera and Field, 1959; Field and Herrera, 1977) except possibly Ureta (1963) who considered the lack of tibial spurs in the *Phulia* series of genera a subfamilial character. As noted by Field (1958) and Field and Herrera (1977), the combinations of characters found in the Andean genera are wildly discordant and make a phylogenetic analysis extremely difficult if not impossible. *Hypsochila* is at the center of most of these discordances. Thus, it groups with *Tatochila* and *Phulia* in uncus shape, with *Phulia*, *Piercolias* Stgr. and the Asiatic *Baltia* Moore in aedeagus, with *Phulia*, *Piercolias*, and *Baltia* in tibial spurs, with nothing in claws, paronychialia, and pulvilli, and with *Theochila*, *Tatochila*, and *Piercolias* in venation. In habitus it closely resembles the *sterodice* Stgr., *xanthodice* Lucas, and *autodice* Hbn. species-groups of *Tatochila*, especially the first, and in genital morphology overall it is quite *Tatochila*-like. It is now evident that *Phulia*, *Infraphulia*, and *Pierphulia* at least share a bizarre set of morphological and behavioral specializations including very slow production of very large eggs, skipper-like larvae with sclerotized cervical shields living in individual silken nests, and rounded skipper- or moth-like

pupae (Shapiro and Courtney, 1986; Shapiro, 1986b). It is also evident that at the enzyme biochemistry level, these genera cluster phenetically very far from *Tatochila*, seriously questioning the hypothesis of monophyly (Geiger and Shapiro, unpublished). Thus it is especially desirable to learn as much as possible about the early stages and biochemistry of the potentially intermediate *Hypsochila*.

Hypsochila ranges from southern Ecuador (G. Lamas, unpubl.) to Tierra del Fuego, at very high elevations in the central Andes to sea level in the far south. Nearly all of the named entities are very rare in collections, and the systematics of the genus (Field and Herrera, 1977) is in an unsatisfactory state because the characters used to distinguish species are weak and the ranges are very poorly known. The best-known *Hypsochila* is the nominate subspecies of *H. wagenknechti* Ureta, primarily because one can drive to its habitat in several Andean passes not far from Santiago, Chile. Even so, its life history has remained unknown until now. Its behavioral ecology is being described quantitatively (Courtney and Shapiro, 1986); qualitative observations bearing on its evolutionary relationships will be presented along with the descriptions of its immature stages, below. These descriptions are based on eggs and larvae collected from the field and eggs from captive females, all from the vicinity of Farellones and La Parva in the Cordón del Cepo, Province of Santiago, 2,500–3,500 m in January and February 1984. Most of these were reared in the field under uncontrolled (ambient) conditions, but those which had not metamorphosed were transferred at the end of the study to Davis, California where they completed larval development at 10L:14D, 23.9°/12.8°C. Preserved early stages are being retained at Davis at this time for comparative studies of chaetotaxy and development. Color descriptions were prepared from life, from preserved (but fresh) material, and from photographs taken in the field. Those in parentheses refer to the system of Kornerup and Wanscher (1978).

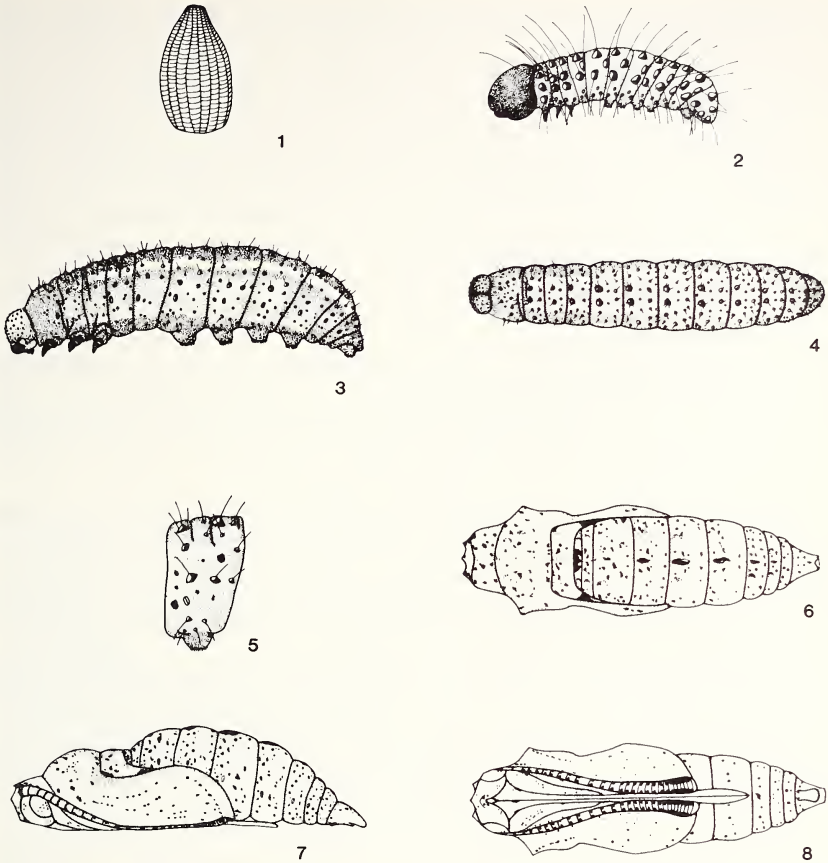
DESCRIPTIONS

Egg (Fig. 1). Erect, fusiform, 0.9×0.35 mm, the chorion sculptured as figured, with about 15 vertical and 30 horizontal ribs, the vertical ribs forming a vaguely beaded corona encircling the micropylar region. Laid on foliage of *Cardamine nivalis* (usually in small clutches) or *Lepidium suffruticosum* (usually singly) (both Cruciferae). Light orange-yellow to orange ("reddish orange," 7A7) when laid, turning slate gray 12 h before hatch. The larva eats a hole in the chorion below the apex, but consumes no more of the eggshell—in this regard differing from *Tatochila* and most Pierini, but resembling *Phulia* and its relatives. Time to hatch, 6 days.

Larva: First instar (Fig. 2). At hatch 1.0 mm at rest. Body buff gray ("pale orange," 5A3) with head dark brownish-black; body becoming gray-green ("grayish green," 26C3) after feeding; with a faint paler pattern of a dorsal and a pair of subdorsal lines, paler below the spiracles. Tubercles few, very large, bearing glandular hairs, black. Excavates pits in leaves and buds. Duration of instar, 2 days.

Second instar. After molt 1.9 mm long. Similar, the pattern more distinct, the tubercles proportionally smaller. Head vaguely mottled with yellowish, ocelli black. True legs brown-black. Length of instar, 3 days.

Third instar. After molt 2.8 mm long. Similar but darker slate gray ("greenish gray," 26C2), the dorsal stripe faint, subdorsals strong and contrasting, a more or less distinct



Figs. 1–8. *Hypsochila wagenknechti wagenknechti* from the Cordón del Cepo, Chile. 1. Egg. 2. Newly hatched larva showing primary tubercles and setae. 3. Mature larva, lateral view. 4. Mature larva, dorsal view. 5. Mature larva, lateral view of seventh segment. 6. Pupa, dorsal view. 7. Pupa, lateral view. 8. Pupa, ventral view.

yellow line through the spiracles, the body paler bluish-gray below; tubercles very distinct, black, bearing dark hairs. Length of instar, 3 days.

Fourth instar. After molt 5.0 mm. Similar to the previous instar. Some individuals show a distinct bright orange-red (“vermilion” = “cinnabar,” 9A8) tinge in the subdorsal and stigmatal lines, and a vague orange tint in the light yellow-brown mottling on the head capsule. Time to molt, 4 days.

Fifth instar (Figs. 3–5). Initial length 14 mm, reaching 20 mm prior to prepupation. Head dark brownish gray mottled with orange-tinted yellow; ocelli black. Body striped lengthwise as follows: a single mid-dorsal line, yellow, usually very faint and commonly entirely absent, surrounded by a broad stripe of slate gray (“medium gray,” 27E1) varying to purplish gray (“grayish magenta,” 14E3), defined outwardly by a

sharply contrasting yellow subdorsal line containing two distinct orange ("fire red," 7A8) spots in each segment; below this again slate to purplish gray, fading into brownish gray (4D2) below the spiracles, the transition area incorporating a series of brilliant red ("cinnabar" = "vermilion," 9A8) spots, one anterior and one posterior to each spiracle, generally strongly contrasting, in a few individuals contained within a diffuse yellow line; venter and prolegs brownish gray (4D2), faintly mottled with black; true legs gray with black mottling. Tubercles large, of three sizes, strongly contrasting, bearing short, stiff, dark hairs. The larva is sluggish, alternating between basking on the plant at low temperatures and concealing itself in the shade in the heat of the afternoon. It makes a silk platform, similar to a molting platform, on which it rests inside the plant, or on the sides of its container. Length of instar, 5–6 days. Final 1–3 fecal pellets pink.

Prepupa. Various disposed, vertical (head up) or horizontal on the container lid, attached by a girdle of silk around the thorax and by the anal prolegs, on a silken platform which in containers may be a reworking of the last larval one, but in nature is made elsewhere after a period of several hours' wandering. Color as in the last instar, the markings becoming less contrasting. Time to pupation 36 hr.

Pupa (Figs. 6–8). Length 16 mm; width at girdle 4.25 mm. Attached as in the prepupa. Front of head and all appendage-cases, including wings, olivaceous brown ("oak brown," 5D6), the antennae strongly black-dotted as shown; top of head creamy white; dorsum of prothorax grayish-white mottled with brown except on the midline; mesothorax similar, the ground color orange-white (5A2), the keel creamy white; metathorax and abdomen gray brown (5D3, "nougat"), carinate, each segment bearing a black line anteriorly on its keel; on either side of the keels a row of large, raised, white tubercles, strongly contrasting; a faint whitish spiracular line; entire dorsum and ventral abdomen with many black tubercles; cremaster gray. Tongue-case moderate, its tip brownish. Frontal and supraocular prominences moderate, wing-bases markedly angular, but no trace of flaring suprspiracular prominences on the abdomen, and the thoracic keel is less developed than in *Tatochila*, though strongly contrasting. Overall, the pupa resembles a more-rounded-than-usual, small *Tatochila*. Like *T. autodice* and *T. blanchardii*, it appears to be an effective bird-dropping mimic, much like the Holarctic *Pieris (Pontia) beckerii* Edwards. Eyes, wings, and body pigmented in that order, white appearing in the wings 30 h and black 16 h before eclosion. This species has a facultative pupal diapause, which under 10L:14D, 21.1°/4.4°C terminated spontaneously in 4 months. We have not reared it directly. Meconium reddish pink.

DISCUSSION

The early stages of *Hypsochila w. wagenknechti*, though superficially fairly similar to *Tatochila*, offer some tantalizing resemblances to the *Phulia* group as well. Specifically: the larva fails to eat its eggshell; it is more sluggish than *Tatochila* and rests on a silken mat when not feeding; and the pupa has lost its suprspiracular prominences and reduced most of the others, including the thoracic keel. *Hypsochila* also has some unique attributes among the Andean *Pierini* reared thus far; it lays its eggs in small batches (but the larvae feed separately), and it has enlarged and very conspicuous larval tubercles. The suggestion of a corona around the micropyle of the

egg is reminiscent of *Phulia* (but not of *Pierphulia*). The loss of the dorsal yellow line in the last instar is very reminiscent of *Tatochila xanthodice* (but not *T. distincta* of the same species group), with which Herrera and Field linked *Hypsochila* in genital morphology. The brilliant red spotting in the last two instars is reminiscent of some *Tatochila* but is a different color, and is unaccompanied by a matching collar.

The chaetotaxy of the Pieridae offers clear opportunities for clarifying phylogenetic relationships, but will require much more study before secure homologies are established and transformation series identified. It may ultimately prove of particular value in ascertaining the phylogenetic position of this enigmatic genus.

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